

STUDIES ON THE GENUS *APHODIUS* OF THE UNITED STATES
AND CANADA (COLEOPTERA: SCARABAEIDAE). IV. A TAXONOMIC
REVISION OF HORN'S GROUP A

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ABSTRACT—Group A of the genus *Aphodius* is redefined, nomenclatural history discussed, and new characters proposed for the Group. I have removed *A. conspersus* Horn from Group A, transferred *A. coloradensis* Horn, *A. dentiger* LeConte, *A. dentigerulus* Brown, and *A. aculeatus* Robinson from other groups into Group A, and describe as new the following 3 taxa: *A. formidatus*, *A. henryi*, and *A. acutissimus*. With these changes Group A contains 10 species. Supposed phylogenetic relationships are discussed and illustrated, the probable evolutionary history of the Group proposed and habitats explained where known.

The present classification of the North American species of *Aphodius* is essentially that of Horn (1887) in which he divided the genus into 4 subgenera, and *Aphodius*, sensu stricto, into 12 groups (A–M). Brown (1927, 1928) revised Group I, series a and b, and followed this (1929b) with a revision of the subgenus *Diapterna* Horn. Van Dyke (1928) combined Horn's Groups G and M and provided a key to species; Saylor (1940) updated this treatment of the 2 Groups. Cartwright (1972) published a key to the species of the *crassulus* Group. With these exceptions, no group of North American *Aphodius* has been taxonomically treated in its entirety since 1887. Schmidt (1922) placed the species in subgenera and described a few new species, but did not change Horn's classification other than nomenclaturally. Many species have been described since, and, though Horn's treatment was excellent and is still useful, it is not possible to accurately identify species of *Aphodius* using only his paper. The revision of Group A presented in this paper is a first step toward an eventual complete reclassification of North American *Aphodius*.

Group A was designated by Horn (1887) for *Aphodius denticulatus* Haldeman and *A. conspersus* Horn. Fall (1907 and 1932) described *A. moquinus* and *A. testaceiventris*, placing them in Group A. No species have been added and the concept of the Group has not been challenged since. In the course of determining the affinities of 3 undescribed species, I have examined Group A critically and the resulting changes in and additions to Horn's classification are presented here. Horn used the appearance of the spines at the apex of the hind tibia as the first character in his key to groups. Groups A to G had these spines short and equal, Groups H to M had them long and un-

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equal. Examination of nearly all of the North American species of *Aphodius* has convinced me that this is a recurring character that has no phylogenetic significance. A primary dichotomy based on this characteristic results in the placing of closely related species in widely separated groups and, conversely, the association of dissimilar species with a single group. This character is, however, of use for separation of species within groups. *Aphodius conspersus* is not a member of Group A as I am defining it, and I here transfer it to Group E which previously contained only *A. rugatus* Schmidt. I transfer *Aphodius coloradensis* Horn, *dentiger* LeConte and *dentigerulus* Brown from Horn's Group I, Series I-d, to Group A. In all characters other than the type of spines on the hind tibiae (overall body form and male fore and middle tibial spurs), these species are closely similar to *denticulatus*. Robinson (1940) described *A. aculeatus* and placed it near *acerbus* Horn in Group K, but it has little in common with the species of Group K and belongs in Group A. With these changes and the addition of 3 new species described here, Group A contains 10 species.

The habits and habitats of most species in Group A are unknown. *Aphodius coloradensis*, *denticulatus*, and *testaceiventris* have been taken in cow dung, but most specimens have been collected at light. Large numbers may be attracted to light in a particular area, yet few or none found associated with cow manure in that same area, suggesting that their preferred habitat is not cow dung. I suspect that they are saprophytic on decaying material in the upper soil layer and are occasionally picked up in or under cow dung. The wide distributions of these 3 species would seem to preclude association with rodents, certainly with any one species of rodent. *Aphodius dentigerulus* has been taken only at burrows of the Black-tailed Prairie Dog, *Cynomys ludovicianus*, and is probably restricted to that habitat. I have suspected *dentiger* to be associated with packrats of the genus *Neotoma*. This suspicion has been confirmed by specimens collected in *Neotoma* nests by C. W. Griffin in 1969, from San Patricio Co., Texas. According to Hall and Kelson (1959), the only species of *Neotoma* there is *micropus* Baird.

I consider Group A to be rather primitive, derived directly from an ancestral form similar to *anthracinus* LeConte and related species which I judge to form the most primitive group of extant species. The male genitalia of members of Group A are not as distinctive for each species as in *anthracinus* and allies but are more so than in more recently evolved groups such as *concausus* Say and allies. In external characteristics, members of Group A are much more diverse than either the *anthracinus* or *concausus* groups. The bulky, unspecialized body form and, for the most part, lack of specialized habitat indicate

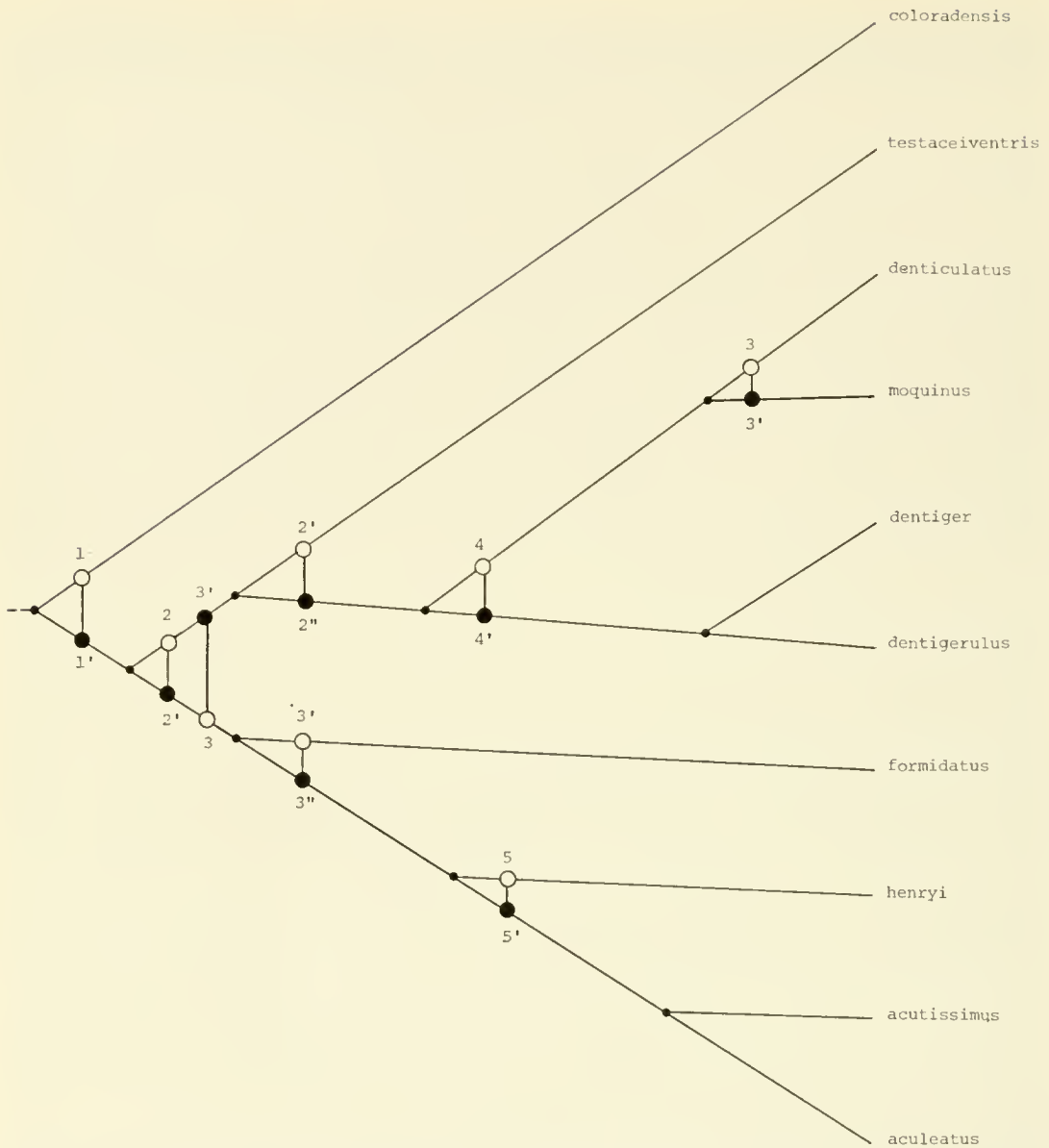


Fig. 1. Reconstructed phylogeny of species taxa of Group A of *Aphodius*. See text for explanation.

that Group A is closely related to the *anthracinus* group. There is little evidence of convergence within the group, but strong evidence of divergence throughout.

I consider *coloradensis*, representing the monobasic *coloradensis* subgroup, the most primitive species because it lacks derived characters. The form of the clypeus in particular is most like that of *anthracinus*. In all other members of Group A, the clypeus possesses more strongly specialized armature (1).

Suspected phylogenetic relationships are summarized in fig. 1, and derived character states used to support these relationships are indicated by parenthetic numbers in the following discussion. In the

figures, derived character states are indicated by black dots and the corresponding number by primes, and in multi-state characters the most derived state is indicated by a double prime.

A major split occurs in the lineage with the *denticulatus* "subgroup" characterized by having oblique clypeal carinae (2') and mostly dark body color (3). This subgroup contains the species *testaceiventris*, *denticulatus*, *moquinius*, *dentiger* and *dentigerulus*. The *acutissimus* subgroup, characterized by the lack of clypeal carinae (2) and mostly pale body color (3'), contains the species *formidatus*, *henryi*, *acutissimus*, and *aculeatus*. Within the *denticulatus* subgroup, I regard *testaceiventris* as most primitive because the clypeal carinae are weakly developed (2') as opposed to the strongly developed carinae of the other members of the subgroup (2''). *Aphodius moquinius* and *denticulatus* have broad, triangular clypeal teeth of the *testaceiventris* type (4), whereas *dentiger* and *dentigerulus* have developed more elongate, somewhat spiniform clypeal teeth (4') and rodent associated habits. The *acutissimus* subgroup contains species almost uniformly pale (3'') in color except *formidatus* (3'), and even *formidatus* is not black or piceous as are most members of the *denticulatus* subgroup. The species are mostly western and all have apparently restricted geographic ranges and probably restricted habitats. *Aphodius formidatus* and *henryi* have the clypeal angles produced, the clypeus appearing quadridentate (5); *acutissimus* and *aculeatus* exhibit a reduction in clypeal armature (5') with that of *aculeatus* in particular strongly reduced. I regard *formidatus* as the most primitive member of the *acutissimus* subgroup because it is most similar to members of the *denticulatus* subgroup in color and clypeal armature. *Aphodius henryi* is primitive in clypeal armature and divergent in possessing elytral vestiture and a strong clypeal ridge. *Aphodius acutissimus* has lost the "quadridentate" appearance of the clypeus but the 2 clypeal teeth are strongly developed with the head in general presenting a formidable appearance. I regard *aculeatus* as the most advanced member of the subgroup because almost all clypeal armature has been lost and the spur of the male middle tibia is weakly modified. Divergent characters of *aculeatus* are the rugose clypeal surface, small size, and lack of dense setae on lateral margin of the pronotum and abdomen.

All species in Group A are native to North America and are restricted to an area from the Great Plains westward to the Pacific Northwest, Nevada and Arizona. They are not represented in California with the exception of *denticulatus* in northern California, or in Mexico, with the exception of *coloradensis* which occurs as far south as Mexico City.

The genus *Aphodius* is largely Holarctic with a few elements extending into Central and South America. With few exceptions (e.g., *coloradensis*) there is no overlap between the northern fauna and that of Mexico and Central America. Members of Group A are most probably survivors of an *Aphodius* fauna that was generally spread throughout the present Great Plains and Great Basin which were forested during the Eocene (Macginitie, 1958). The ensuing drying and cooling climate that followed during and after the Oligocene resulted in the forest being replaced by grassland (well developed by the Pliocene) and desert (except at high elevations). This in turn reduced the favorable habitat for species of *Aphodius*, causing the isolation and resultant speciation of Groups of *Aphodius*. At least two species of Group A, *dentigerulus*, and *dentiger*, evolved the habit of using the shelter and food of rodent burrows and nests.

By the upper Pliocene, conditions were essentially the same as those at present (Frye and Leonard, 1957) so the modern species of Group A have evolved to their present condition since that time. The climatic fluctuations of the Pleistocene strongly influenced the present distribution of members of Group A. Some species (*coloradensis*, *testaceiventris*) were probably least affected, but I regard the speciation of the *acutissimus* subgroup now evident to be a result of climatic changes during that period. The present distribution of *testaceiventris* (fig. 27) shows a wide gap between southern Texas and Colorado. I cannot satisfactorily separate specimens from the 2 extremes on a morphological basis and am regarding them as the same species. This separation, if not an artifact of inadequate sampling, is relatively recent and it may be that differences will evolve in the future to the point where specimens from southern Texas are morphologically separable from Colorado and Kansas specimens. The distribution maps of *coloradensis* and *denticulatus* (fig. 26, 27) show that *denticulatus* is primarily a Great Basin species whereas *coloradensis* occurs mostly east and south of the Great Basin. The 2 species are nearly completely allopatric. *A. coloradensis* is either more tolerant of a greater range of climatic conditions (occurring from Alberta to Mexico City) than *denticulatus*, or *denticulatus* has adapted to a more restricted habitat (such as rodent burrows or nests) than that of *coloradensis*.

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GROUP A

Body robust, fimbriate with setae, convex, elongate; posterior pronotal border margined; anterior clypeal margin dentate, either quadridentate, or bidentate with anterolateral angle projecting (except *aculeatus*, *acutissimus* and *coloradensis*); median area of clypeus with ridge, carinate or not; frontal suture raised, distinct; short outer spur of male middle tibia modified (thickened, or apex truncate, or appearing bifurcate, or simply bent inward).

Except for 3 species, *coloradensis*, *acutissimus* and *aculeatus*, the species in Group A have more or less quadridentate anterior clypeal margins. *Aphodius coloradensis* is closely related to *testaceiventris* despite having a feebly bidentate or biangulate clypeal margin. The overall body form and the modifications of the male fore and middle tibial spurs of *coloradensis* indicate a close relationship to *denticulatus* and *testaceiventris*. Both *acutissimus* and *aculeatus* lack certain characteristics of Group A as defined here. Both have bidentate clypeal margins, but *acutissimus* has the median clypeal ridge reduced. The male tibial spurs in both species are not as strongly modified as in the rest of the group. The facies of both species are typical of Group A however, and they fit more readily here than in any other group of *Aphodius* presently defined.

Schmidt (1922) placed *denticulatus*, *moquinius* and *conspersus* in his subgenus *Tetraclipeoides* along with a species from Cuba and another from Senegal. As in Horn's classification, Schmidt's reliance on one character (in this case the quadridentate clypeus) caused him to group species of different phyletic lineages together. He placed *coloradensis* and *dentiger* in the subgenus *Pseudagolius*. As previously indicated (Gordon, 1973), the North American species do not conform well to the subgenera of *Aphodius* as used by Schmidt (1922), and I do not formally place new species of *Aphodius* in subgenera.

KEY TO SPECIES OF GROUP A

1. Apical margin of clypeus between teeth with 2 short, oblique carinae forming a triangle on surface of clypeus (fig. 10) 2
- Apical margin of clypeus between teeth lacking oblique carinae (fig. 4) 5
2. Apical clypeal armature consisting of 2 short, bluntly rounded teeth, anterolateral angle slightly produced, rounded (fig. 11) 3
- Apical clypeal armature consisting of 2 generally acute, triangular teeth, anterolateral angle distinctly produced, angulate or dentate (fig. 8) 4
3. Clypeus depressed, flattened anterior to median ridge, densely punctured, smooth between punctures (fig. 10) *dentiger* LeConte
- Clypeus not depressed or flattened anterior to median ridge, roughly sculptured, rugose (fig. 13) *dentigerulus* Brown

4. Clypeus appearing quadridentate, anterolateral angle acute (fig. 8); male outer tibial spur broad, with lateral tooth (fig. 9) *denticulatus* Haldeman
- Clypeus not appearing quadridentate, anterolateral angle abrupt; male outer tibial spur slender, hooked inward at apex *moquinus* Fall
5. Anterolateral angle of clypeus rounded, angulate or produced (fig. 5) 6
- Anterolateral angle of clypeus smoothly rounded or nearly straight, not produced (fig. 2) 8
6. Anterolateral angle of clypeus acute or angulate, more prominent than anterior teeth (fig. 5) *testaceiventris* Fall
- Anterolateral angle of clypeus less prominent than anterior teeth 7
7. Pubescence not visible on 10th elytral interval or apical declivity of elytron; color dark reddish brown; length usually more than 5.40 mm *formidatus*, new species
- Pubescence visible on 10th elytral interval and on apical declivity of elytron; color light reddish brown; length usually less than 5.40 mm *henryi*, new species
8. Color piceous to black; clypeal teeth reduced, angulate or rounded apically (fig. 2); anterolateral angle evenly rounded *coloradensis* Horn
- Color light reddish brown to yellowish brown; clypeal teeth prominent or reduced, anterolateral angle evenly rounded or nearly straight 9
9. Length 5.50 mm or more; clypeus smooth, median ridge reduced, anterior teeth prominent, strongly reflexed (fig. 20) *acutissimus*, new species
- Length less than 5.00 mm; clypeus rough, rugose, with median ridge, anterior teeth reduced, feebly reflexed (fig. 22) *aculeatus* Robinson

Aphodius coloradensis Horn

fig. 2, 3, 26

Aphodius coloradensis Horn, 1870:130. Horn, 1887:45.

Aphodius (Pseudagolius) coloradensis: Schmidt, 1913:150. Schmidt, 1922:237.

Aphodius flohri Bates, 1887:86. Schmidt, 1913:150, established synonymy.

Remarks: The clypeus of this species is not armed with the distinct teeth and angulations possessed by most species of this group, and the clypeal ridge is reduced to a convex swelling. In all other respects, however, including overall appearance, *coloradensis* is a typical member of Group A, resembling *denticulatus* and *testaceiventris* in color and form. The clypeal teeth are small and blunt, often appearing as feeble, angulate projections rather than teeth; the anterolateral angle is not apparent, the clypeal border from anterior tooth to posterolateral angle is smoothly rounded (fig. 2). The outer spur of the middle tibia of the male is truncate apically, the inner apical angle bent inward (fig. 3).

The habitat preference of *coloradensis* is unknown but is probably as discussed for *denticulatus*. The range of *coloradensis* is greater than that of other native North American *Aphodius* except *vittatus* Say, extending from Alberta, North Dakota and Iowa to Mexico City.

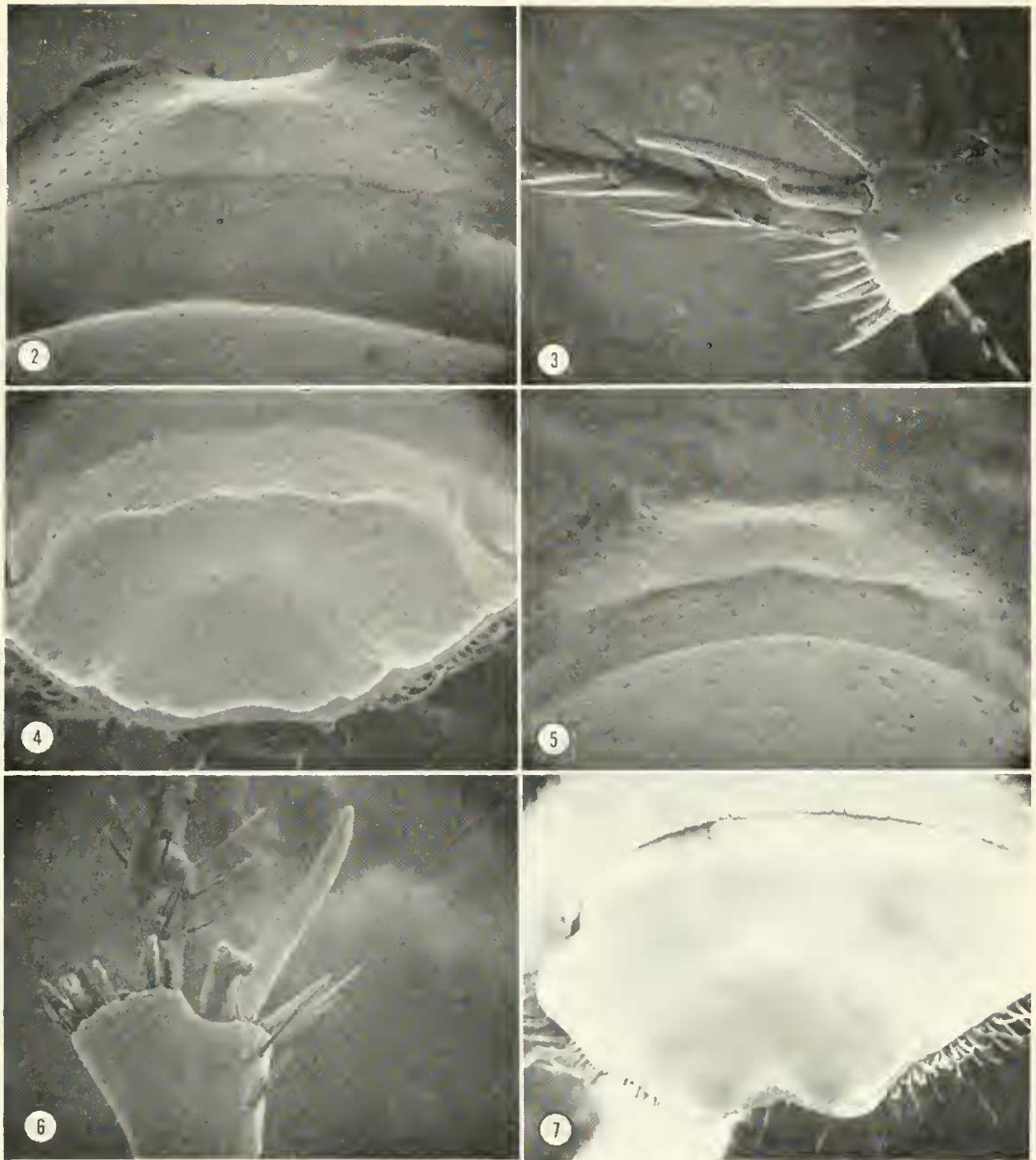


Fig. 2-7. Dorsal views of head, views of apices of middle tibiae. 2-3, *Aphodius coloradensis*. 4-6, *Aphodius testaceiventris*. 7, *Aphodius denticulatus*.

The lectotype (here designated and so labeled) of *Aphodius flohri* Bates in the British Museum (N. H.) has been examined. It is from Durango City, Mexico, and is, as indicated by Schmidt (1913), the same species as *coloradensis*. The lectotype is labeled "Type (white disc with orange border) Durango City, Mexico, Hoge/flohri Bates." A specimen in the USNM collection bearing the same labels except "U.S.N.M. Paratype No. 49713" is here designated paralectotype and so labeled. Horn (1870) plainly indicated that he saw more than one type-specimen of *coloradensis*, so the single female remaining in his collection at the MCZ, labeled "Col./Type No. 3591, *Aphodius*

coloradensis G. H. Horn/A. Coloradensis Horn" is here designated LECTOTYPE.

Specimens examined: Total 324 (fig. 26) (Mexican localities not included). ALBERTA: Medicine Hat. ARIZONA: Chiricahua Mts.; Flagstaff; Fort Grant; Gila Co.; Nogales; Palmerlee; Portal, S. W. Research Station; Santa Rita Mts.; White Mts.; Williams. COLORADO: Buena Vista; Colorado Springs; Denver; Florissant, La Plata Co., Durango; Mesa Verde; Pueblo; Trinidad. IOWA: Iowa Co. MINNESOTA: Alexandria; Glenwood. MONTANA: Havre. NEBRASKA: Lincoln; Meadville. NEW MEXICO: Alamogordo; Gallup; Koehler; Mescalera Res. NORTH DAKOTA: Eddy Co., Lake Coe; Fargo; Northwood, Goose River; Richland Co.; Walcott. OKLAHOMA: Fort Sill. SOUTH DAKOTA: Britton; Brookings; Chamberlain. WYOMING: Cheyenne; Laramie.

Aphodius testaceiventris Fall

fig. 4-6, 27

Aphodius testaceiventris Fall, 1932:185.

Remarks: At first glance, *testaceiventris* appears to be conspecific with *denticulatus*, but *testaceiventris* lacks the oblique clypeal carinae (fig. 4, 5), and the outer spur of the male middle tibia is slender and more or less truncate apically (fig. 6). In addition, the average size of *testaceiventris* is smaller than that of *denticulatus*, and the anterolateral clypeal angle is more prominent than the clypeal teeth. The 2 species are nearly allopatric.

No more is known of the habits of this species than is known of *denticulatus*; speculations as discussed under *denticulatus* apply here.

Fall (1907) stated that he had received 3 specimens from F. H. Snow. Of these, only a single female remains in his collection. It is labeled "Hamilton Co., Ks., 3350 ft., F. H. Snow/June '02/n. sp. near *denticulatus*/Type *testaceiventris*/M.C.Z. Type 24763." This specimen is here designated lectotype and is so labeled. As indicated in fig. 27, there is a wide gap in the distribution of *testaceiventris* between southern Texas and Colorado and western Kansas. Specimens from south Texas are slightly larger, the clypeal armature is more pronounced and the elytral intervals are usually more convex. These differences are minor however, and the male genitalia and tibial spurs are the same, so I consider this to be one species. There is a male in the USNM type collection, from Brownsville, Texas, labeled "Holotype, *Aphodius texana*, Mark Robinson". This is apparently a manuscript name as I cannot find a description in the literature. The head and thorax are missing, but the elytra, male genitalia and tibial spurs all indicate that the specimen is *testaceiventris*.

Specimens examined: Total 46 (fig. 27). COLORADO: Baca Co; Boulder; Canon City; Cherry Creek; Greeley. KANSAS: Hamilton; Meade. TEXAS: Brownsville; College Station; Palo Duro Canyon; Sonora; Uvalde; Zavalla Co., Nueces River.

Aphodius denticulatus Haldeman

fig. 7-9, 27

Aphodius denticulatus Haldeman, 1848:104. Horn, 1870:116. Horn, 1887:9.*Aphodius (Tetraclipeoides) denticulatus*: Schmidt, 1913:139. Schmidt, 1922:156.

Remarks: This species has the most pronounced clypeal armature of any species in Group A, approached in this respect only by *moquinius*, *testaceiventris* and *formidatus*. The anterolateral angle of the clypeus is less prominent than the anterior teeth and is strongly reflexed, apically acute or at least sharply angulate (fig. 7, 8). The outer apical spur of the male middle tibia is strongly thickened and laterally toothed (fig. 9), much more strongly modified than in any related species.

Specimens of *denticulatus* in the USNM collection were mostly taken at light, but a few were collected at horse dung, cow dung and one specimen from a dead rabbit. The collecting of this species at dung of domestic animals is so rare as to indicate that it is not the normal habitat. *A. denticulatus* is probably saprophytic on decaying plant material in the upper soil layer. It is also possible that it is associated with rodents, but if so, the wide distribution of *denticulatus* dicates that several species of rodents would have to be involved, whereas other rodent associated *Aphodius* are usually nearly completely host specific.

The type is a female in the MCZ labeled "(green disc)/Type 8353 (red paper)/*H. denticulatus* Hald." It is apparent from Haldeman's description that he had only a single specimen so this must be considered the holotype.

Specimens examined: Total 157 (fig. 27). ALBERTA: Medicine Hat. CALIFORNIA: Hackamore. IDAHO: Bingham Co; Burley; Custer Co., Mackay; Milner; Mullan; Payette; Pocatello. MONTANA: Havre; Helena. NEVADA: Humboldt Co., Martin Cr. OKLAHOMA: El Reno. OREGON: Baker Co., Unity; Dalles. UTAH: Lookout Mt.; Mt. Timpanogos; Park Valley; Promontory; Tooele Co., Dugway Proving Ground; Vernal. WASHINGTON: Henifer (not located). WYOMING: Carbon Co.; Green River; Lamont; Laramie; Medicine Bow; Rock Springs.

The Oklahoma record listed above may be mislabeled as it is widely disjunct.

Aphodius moquinius Fall

fig. 27

Aphodius moquinius Fall and Cockerell, 1907:242*Aphodius (Tetraclipeoides) moquinius*: Schmidt, 1913:139. Schmidt, 1922:156.

Remarks: The oblique clypeal carinae are reduced, extending only slightly inward from the clypeal apex, and are intermediate in this respect between *denticulatus* and *testaceiventris*. The median clypeal ridge is strongly carinate, much more so than in *denticulatus* or *testa-*

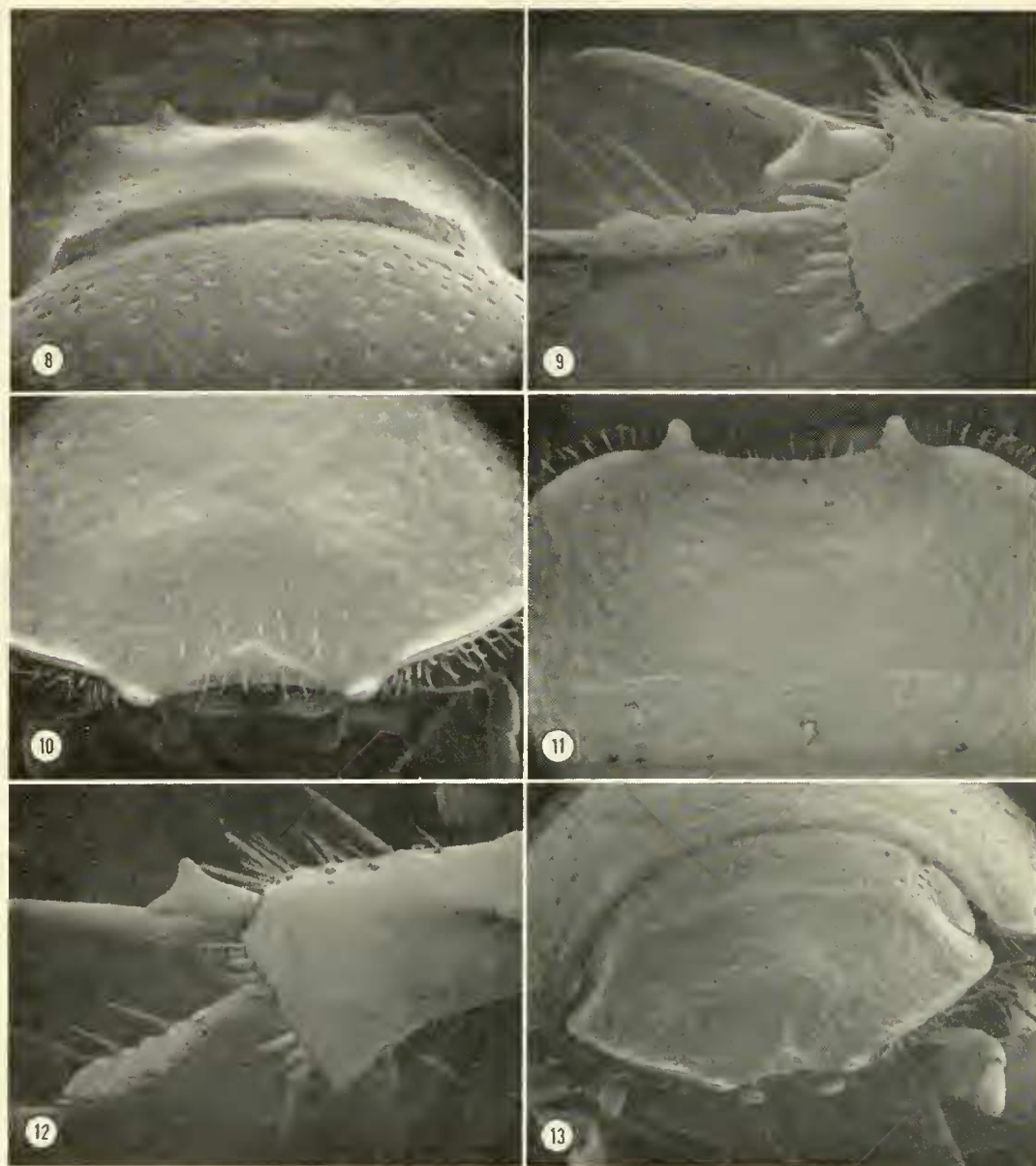


Fig. 8-13. Dorsal views of head, views of apices of middle tibiae. 8-9, *Aphodius denticulatus*. 10-12, *Aphodius dentiger*. 13, *Aphodius dentigerulus*.

ceiventris, and the overall color is light yellowish brown. The outer apical spur of the male middle tibia is slender and apically truncate.

The habitat is unknown and only 3 specimens have been recorded, all from Holbrook, Arizona. Fall (1907) had a male and a female of this species (a pair sent him by Wickham) but only the male remains in his collection. This male, labeled "Holbrook, Ariz./IV-13-VII/moquinus Type/M.C.Z. Type 24758" is here designated LECTOTYPE and so labeled.

Specimens examined: Total 3 (fig. 27). ARIZONA: Holbrook.

Aphodius dentiger LeConte

fig. 10–12, 28

Aphodius dentiger LeConte, 1858 (1859):65. Horn 1870:130. Horn, 1887:45. Brown, 1929:209.

Aphodius (Pseudagolius) dentiger: Schmidt, 1913:150. Schmidt, 1922:237.

Remarks: This species is very closely allied to *dentigerulus* Brown, but, in addition to the differences presented in the key, *dentiger* is larger (4.80 mm or more in length), the elytral intervals are more densely and obviously punctate, and the male anterior tibial spur is distinctly bent inward at the apex. Brown (1929a) noted that the outer spur of the middle tibia of the male was truncate apically in *dentigerulus*, dilated and emarginate in *dentiger*, but I've examined several large series of *dentigerulus* and the shape of this spur varies from truncate to almost exactly like that found in *dentiger*. Views of the head and apex of the middle tibia are presented in fig. 10–12.

Aphodius dentiger is a rarely collected species that is associated with packrats of the genus *Neotoma* Say and Ord. The type is a unique male in the LeConte collection (MCZ), labeled "(silver disc)/A. dentiger LeC., Copper mines Webb/Type 3745 (red paper)." This specimen is the holotype because LeConte specifically stated that he had only one specimen from Dr. Webb collected at the "copper mines of the Gila". Copper mines in the vicinity of Globe (Gila Co.) and Morenci (Greenlee Co.) may have been in existence long enough to have been type-localities of species described by LeConte, but the type-locality could be one of many places along the Gila in Arizona or New Mexico.

The locality "Sharpsburg, Texas", listed below doesn't appear on current maps, but old maps and gazetteers place it in San Patricio Co.

Specimens examined: Total 13 (fig. 28). ARIZONA?: "Copper mines of the Gila" (type loc.). NEW MEXICO: Clovis. TEXAS: Brownsville; Corpus Christi; San Patricio Co., US Hwy. 77. 1.2 mi. from Int. with State Hwy. 9, from *Neotoma* nest; Sharpsburg.

Aphodius dentigerulus Brown

fig. 13–15, 28

Aphodius dentigerulus Brown, 1929a:208. Helgeson and Post, 1967:38.

Remarks: *Aphodius dentigerulus* resembles only *dentiger* in the group of species having oblique clypeal carinae. See remarks under that species. Views of the head and apex of the middle tibia are presented in fig. 13–15. Brown's specimens were from Oklahoma, and he stated that they occurred "in the burrows of the common prairie dog" (*Cynomys ludovicianus ludovicianus* Ord.). The species has been recorded since by Helgeson and Post (1967) from prairie dog burrows in south-

western North Dakota. I have taken it at the same locality in 1969 and in southwestern South Dakota in 1973 in prairie dog burrows. The species is apparently restricted to the burrows of the Black-tailed Prairie Dog and may be found in tremendous numbers in May and June. The populations disappear during the dry periods of the summer, and I have not been able to collect this species in the fall. *Aphodius dentigerulus* is an external associate of the prairie dog in that this species does not seem to occur deep within the burrow but feeds on dung pellets around the mound, buried within the mound, or just within the burrow entrance.

The holotype of *dentigerulus* is No. 2946 in the Canadian National Collection, Ottawa. The type-locality is Noble Co., Oklahoma, and I have examined 10 paratypes from that locality in the USNM collection.

Specimens examined: Total 331 (fig. 28). NORTH DAKOTA: Billings Co., Theodore Roosevelt Memorial Park. OKLAHOMA: Noble Co.; Noble Co., 101 Ranch; Noble Co., Otoe Pasture. SOUTH DAKOTA: Custer State Park.

Aphodius formidatus Gordon, new species
fig. 16-17, 23, 28

Holotype: Male, length 6.00 mm, greatest width 2.90 mm. Form elongate, nearly parallel sided, widest just posterior to middle of elytra. Color dark reddish brown except ventral surface paler yellowish brown. Head shining, a raised ridge extending across front, ending in small tubercle at each end, feebly tuberculate medially; clypeus coarsely punctured, median ridge present, apex emarginate between 2 strong, triangular teeth, lateral margin uneven, deeply excised as in fig. 16. Pronotum smooth, shining, densely, coarsely punctured, punctures separated by less than the diameter of a puncture; anterolateral angle abrupt, lateral border evenly curved, strongly margined, fimbriate with short setae, posterolateral angle broadly rounded, posterior border distinctly margined. Elytron smooth, shining, lateral margin fimbriate with short setae, striae deep, distinct, strial punctures fine, separated by the diameter of a puncture; intervals slightly convex, each interval with fine punctures arranged in 2 irregular rows. Ventral surface shining medially, alutaceous laterally; metasternum with some coarse, irregularly scattered punctures medially. Upper surface of fore tibia with reticulate surface sculpture composed of elongate cells oriented parallel to axis of tibia, lateral teeth strong, posterior tooth basad of middle of tibia, apical spur dorsoventrally flattened, apex hooked inward; apex of middle tibia with 2 spurs, outer spur $\frac{1}{2}$ the length of inner, robust, apex bent inward (fig. 17), inner spur slender, straight, apex pointed; apex of hind tibia fringed with long, unequal spines. Anterior tarsus with basal segment $\frac{1}{2}$ as long as segment 2, segments 2-4 subequal, 5th segment slightly longer than segment 4; middle and hind tarsi with basal and apical segments long, subequal, middle 3 segments subequal, each segment $\frac{3}{4}$ as long as 5th. Abdominal sterna dull, alutaceous, pubescent. Genitalia as in fig. 23.

Type-material: Holotype, ♂, Texas, Garza Co., 12 mi. N. Post,

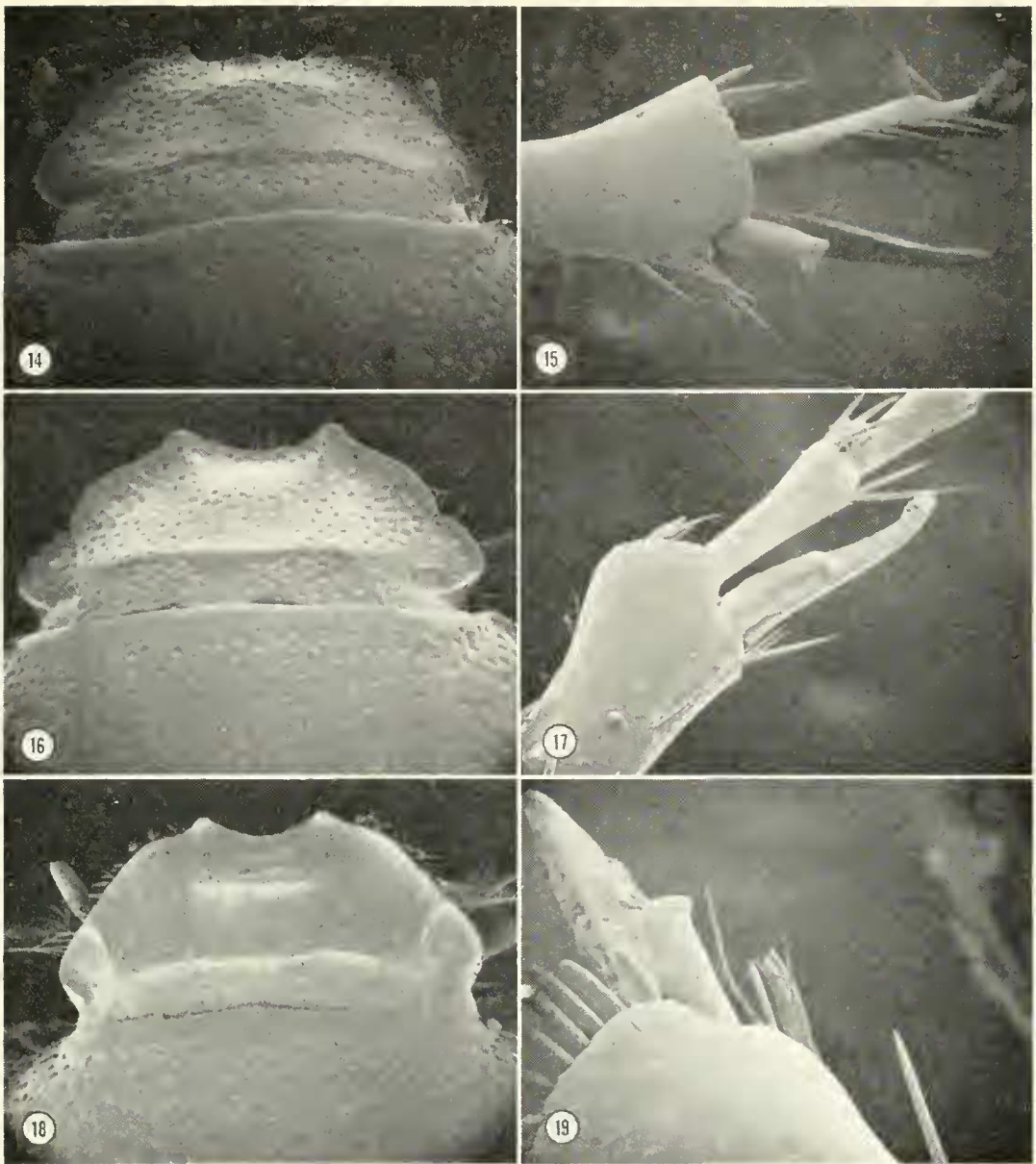


Fig. 14-19. Dorsal views of head, views of apices of middle tibiae. 14-15, *Aphodius dentigerulus*. 16-17, *Aphodius formidatus*. 18-19, *Aphodius henryi*.

Montgomery Ranch, X-2-1970, C.R. Ward, at u.v. light (USNM 73406). Paratypes, 6 ♂, with same data as holotype (USNM) (fig. 28).

Variation: Length ranges from 5.40 mm to 6.00 mm, greatest width from 2.52 mm to 2.90 mm.

Remarks: Of the previously described species, *denticulatus* and *testaceiventris* most nearly resemble *formidatus*. In addition to the characters used in the key, the body of *formidatus* is more elongate and parallel than that of either of the other 2 species; the anterior tibial spur of the male is flattened and bent inward in *formidatus*, simply thickened and very slightly or not at all bent inward in the

others; the outer apical spur of the middle tibia of the male is slightly bent inward at the apex in *formidatus*, not secondarily toothed or apically truncate as in *denticulatus* or *testaceiventris*. In addition, the anterior clypeal angles are rounded in *formidatus*, acute or sharply angulate in both of the other species.

All type-specimens are males taken at u.v. light and this may indicate that the females are not attracted to light or not present.

The specific name is a Latin adjective (past participle of *formido*) referring to the formidable appearance presented by the clypeal margin.

Aphodius henryi Gordon, new species
fig. 18, 19, 24, 28

Holotype: Male, length 5.41 mm, greatest width 2.65 mm. Form elongate, robust, widest posterior to middle of elytra. Color light reddish brown, ventral surface except tibiae light yellowish brown. Head shining, a raised ridge extending across front, ending in small tubercle at each end; clypeus finely, sparsely punctured, short, median, carinate ridge present, ridge weakly emarginate medially, apex emarginate between 2 strong, triangular, slightly recurved teeth, anterolateral angle broadly angulate, reflexed, lateral margin reflexed (fig. 18), not excised. Pronotum smooth, shining, coarsely punctured, punctures separated by less than to $2\times$ the diameter of a puncture; anterolateral angle abrupt, lateral border evenly curved to midpoint, fimbriate with long, dense setae, slightly explanate near anterolateral angle, posterolateral angle broadly rounded, posterior border distinctly margined. Elytron shining, feebly alutaceous, fimbriate with long setae, striae shallow, strial punctures fine, separated by the diameter of a puncture; intervals flat, nearly impunctate, each interval with an occasional puncture, entire 10th interval and all intervals on apical declivity with short, distinct pubescence. Ventral surface shining medially, alutaceous laterally; metasternum with several coarse, irregularly scattered punctures medially. Fore tibia as described for *formidatus* except apical spur short, stout, curved ventrally; middle tibia as described for *formidatus* except outer spur shorter, broader, apex only slightly bent inward, inner spur curved (fig. 19); apex of hind tibia fringed with short, equal spines. Anterior tarsus with basal segment nearly as long as segment 2, segments 2-4 subequal, fifth segment $\frac{1}{4}$ longer than segment 4; middle and hind tarsi with basal segment as long as segments 2-3 combined, segments 2-4 subequal, 5th segment $\frac{1}{3}$ longer than segment 4. Abdominal sterna dull, alutaceous, pubescent. Genitalia as in fig. 24.

Allotype: Female, length 4.60 mm, greatest width 2.41 mm. Similar to male except anterior spur of fore tibia more slender, elongate; outer spur of middle tibia slender, apex acute, not bent.

Type material: Holotype, ♂, Utah, 14 mi. S. Hanksville, Fairview Ranch, 21-VII-1973, Robert Gordon, collected in sand-oak area, dead under dry cow chips (USNM 73407). Allotype, ♀, same data as holotype (USNM). Paratypes, 17 (9 ♂, 8 ♀): 10 with same data as holotype; 5, Utah, Hanksville, VIII-9-1968, A.T. Howden (CNC) (HH) (USNM). (fig. 28).

Variation: Length ranges from 4.00 mm to 5.41 mm, width from 2.10 mm to 2.65 mm.

Remarks: The presence of distinct pubescence on the apical declivity of the elytron and the 10th elytral interval along with the carinate, medially emarginate clypeal ridge distinguish *henryi* from any other member of Group A. It is a relatively pale species, as are most desert dwelling *Aphodius*, similar in this respect to *acutissimus* and *aculeatus*. All type-specimens were collected dead under dry cow chips so the period of flight activity for this species is obviously earlier in the year than July and August. Because of the dry desert conditions of the Hanksville area, most of the specimens collected were in good condition, either intact or missing parts of the legs. The collection site is, in general, a sandy sagebrush desert area, and the specimens were collected along a dry, sandy wash lined with dwarf Gambel's Oak (*Quercus gambeli* Nutt.) ranging from a few inches to 6 feet in height. These dead specimens almost certainly had taken refuge under the cow dung and were not using it as a food source. This species is either saprophytic as postulated for *denticulatus*, or associated with a species of rodent. Throughout the area described above are rock ledges with numerous packrat (*Neotoma* sp.) nests. It is quite possible that *henryi* is associated with these packrats, particularly since another species of Group A, *dentiger*, is associated with a species of packrat.

The specimens taken in 1968 were referred to me by Henry Howden and the species is named both for him and for the Henry Mountains as the type-locality is at the northern edge of these mountains.

Aphodius acutissimus Gordon, new species

fig. 20-21, 25-26

Holotype: Male, length 5.60 mm, greatest width 2.65 mm. Form elongate, slender, widest posterior to middle of elytra. Color light reddish brown, ventral surface except tibiae light yellowish brown. Head shining, coarsely punctured, punctures separated by the diameter of a puncture or less, frontal ridge sharply raised, not tuberculate; median area of clypeus nearly impunctate, no median ridge present, surface slightly convex, apex deeply emarginate between 2 large, triangular, slightly recurved teeth, anterolateral angle obsolete, lateral margin reflexed as in fig. 20. Pronotum smooth, shining, coarsely punctured, punctures separated by less than to twice the diameter of a puncture; anterolateral angle rounded, projecting, lateral border slightly flattened, straight medially, finely margined, fimbriate with short setae, posterolateral angle rounded, posterior border finely margined. Elytron shining, lateral border fimbriate with short setae, stria distinctly impressed, strial punctures coarse, separated by twice the diameter of a puncture; intervals convex, each interval with a row of irregularly spaced fine punctures. Ventral surface shining medially, alutaceous laterally.

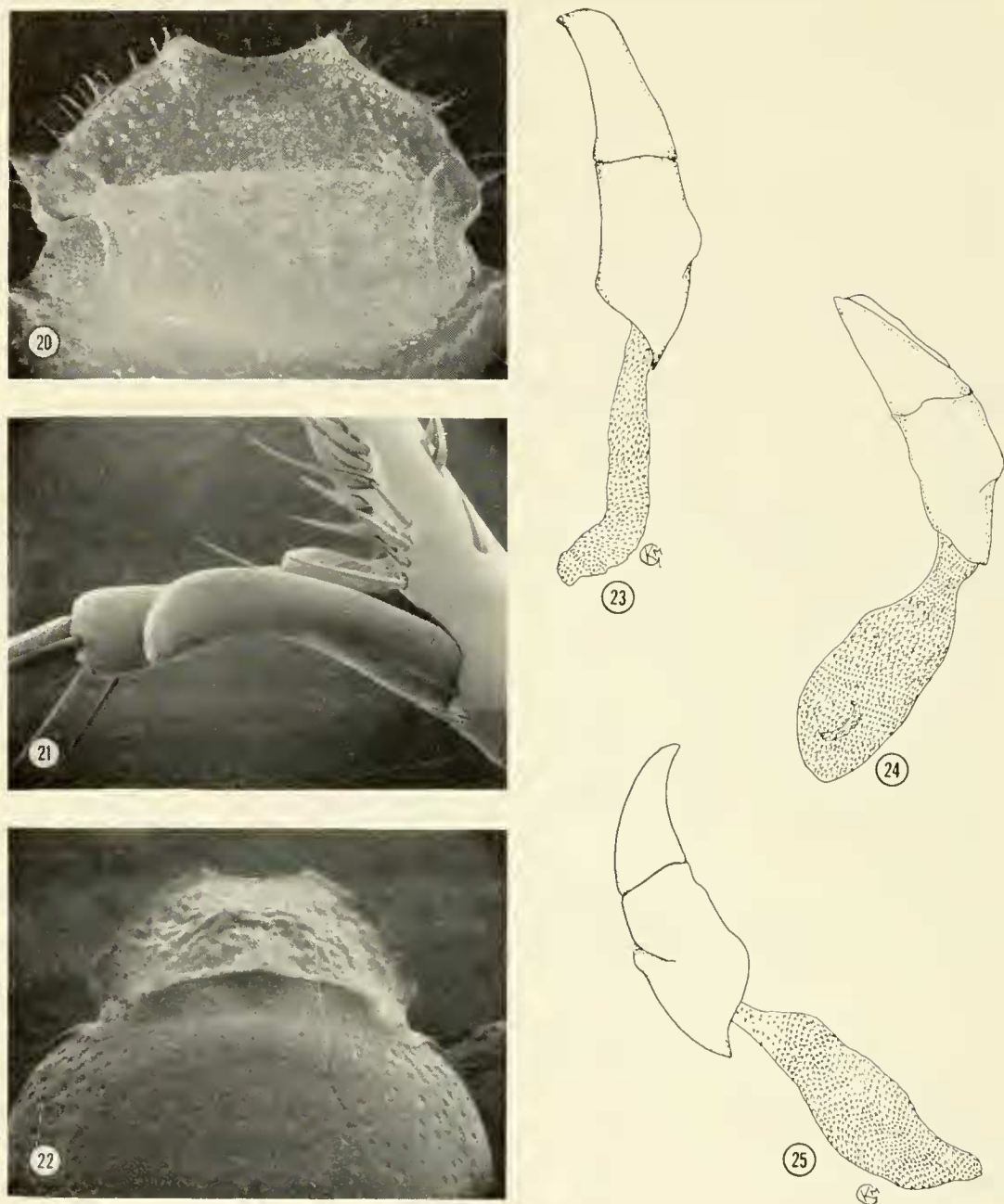


Fig. 20–25. Dorsal views of head, view of apex of middle tibia, lateral views of male genitalia. 20–21 and 23, *Aphodius acutissimus*. 22, *Aphodius aculeatus*. 24, *Aphodius henryi*. 25, *Aphodius acutissimus*.

Fore tibia as described for *formidatus* except anterior half of upped surface polished, apical spur long, thickened, abruptly bent inward at apex (fig. 21); middle tibia with apical spur broken; apex of hind tibia fringed with long, unequal spines. Anterior tarsus as described for *formidatus*; middle and hind tarsi as described for *formidatus*. Abdominal sterna dull, alutaceous, coarsely, sparsely punctured, pubescent. Genitalia as in fig. 25.

Allotype: Female, length 6.00 mm, greatest width 2.91 mm. Similar to male except anterior spur of fore tibia slender, acute apically, not bent inward at apex.

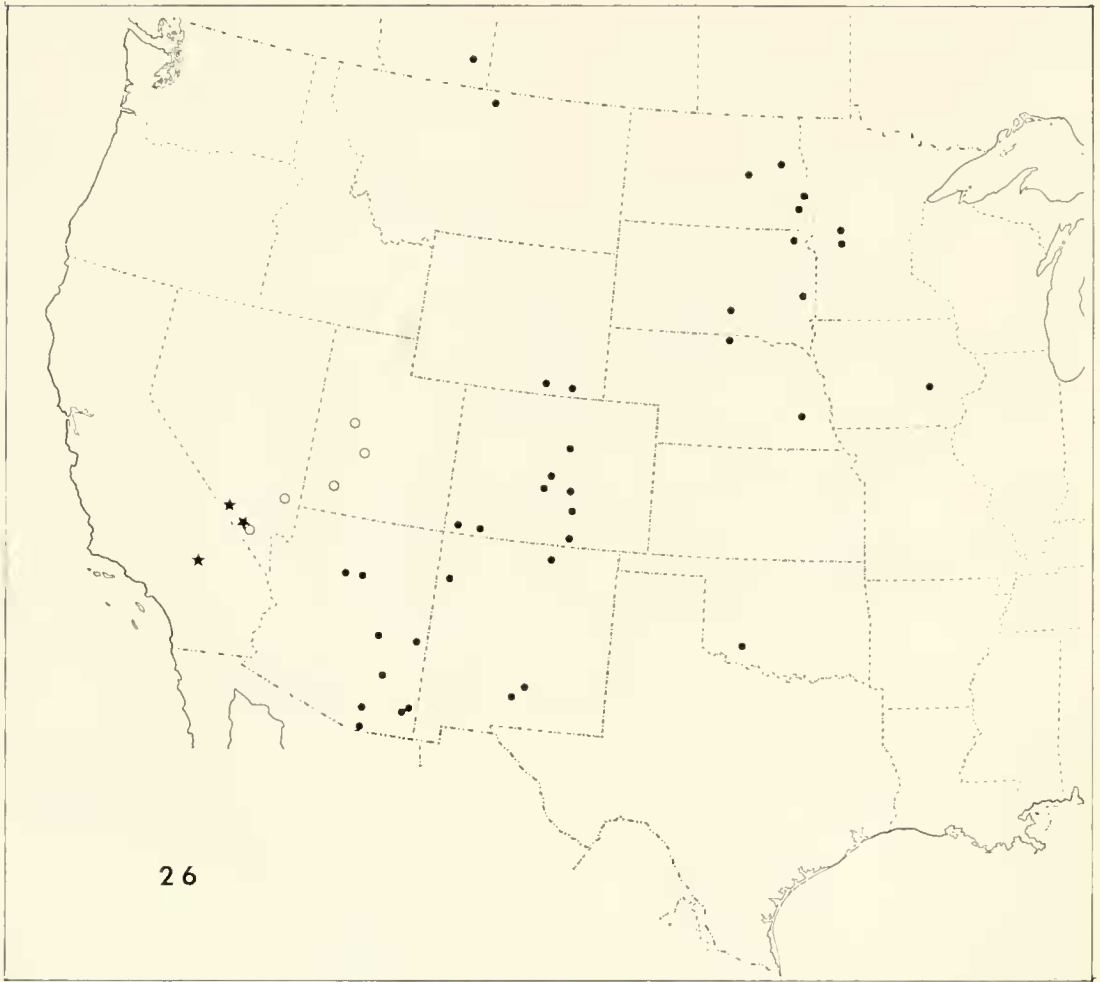


Fig. 26. Distribution of *Aphodius coloradensis* (dots), *Aphodius acutissimus* (stars), and *Aphodius aculeatus* (circles).

Type material: Holotype, ♂, Nevada, Nye Co., Pahrump, IX-11-1960, R. C. Bechtel, at u.v. light (USNM 73408). Allotype, ♀, same data as holotype. Paratypes (50), 4 ♀, same data as holotype; 1 ♀, Nevada, Nye Co., Amargosa Desert sand dunes, 11-X-1972, u.v. light, Derham Giuliani; 21 ♂, 24 ♀, California, Yermo, IX-29-1939, W. M. Pearce. (CAS) (NDA) (USNM) (fig. 26).

Variation: Length ranges from 5.60 mm to 7.00 mm, width from 2.65 mm to 3.41 mm. The clypeal teeth are larger and sharper on some specimens than on others.

Remarks: The absence of a central clypeal ridge and the presence of only 2 teeth on the clypeal margin distinguish *acutissimus* from other species in Group A. In both respects this species most nearly resembles *coloradensis* Horn, but *coloradensis* is a dark brown to black species and the clypeal teeth are indistinct, not prominent. The type-series was taken at light and no habitat information is available.

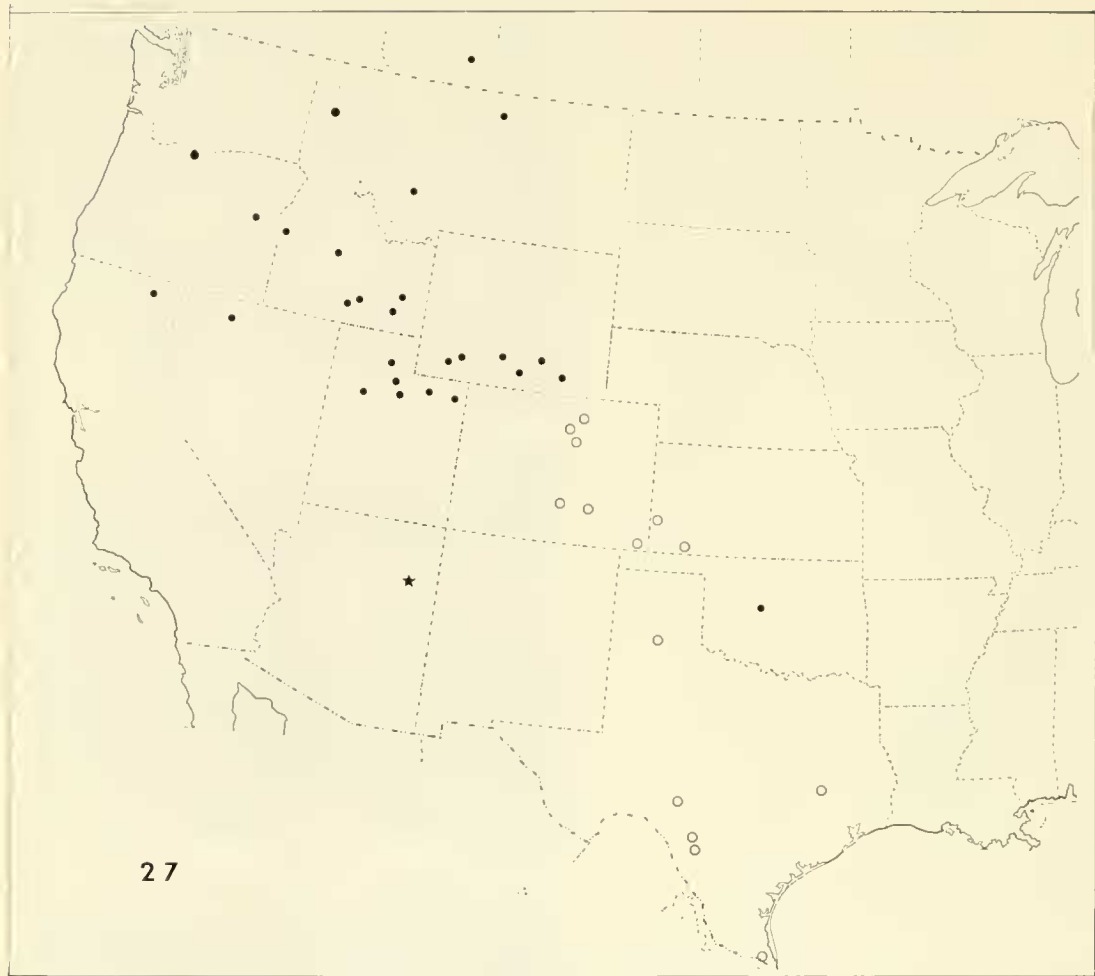


Fig. 27. Distribution of *Aphodius testaceiventris* (circles), *Aphodius denticulatus* (dots), and *Aphodius moquinius* (star).

The species name is a Latin adjective referring to the prominent, acute clypeal teeth.

Aphodius aculeatus Robinson
fig. 22, 26

Aphodius aculeatus Robinson, 1940:143

Remarks: This is the most atypical member of Group A because of the combination of small size, pale color and reduced clypeal armature. I place it in this Group because of the carinate clypeal ridge, raised frontal suture and dentate clypeal margin. The body form and facies are also characteristic of Group A despite the small size (4.30 mm or less in length). The clypeus of *aculeatus* is rugosely sculptured, the ridge carinate and the anterolateral angle rounded (fig. 22). The color is light reddish brown as in *henryi*.

The few specimens that have been collected have all been taken at light. It is probable that *aculeatus* is associated with some species

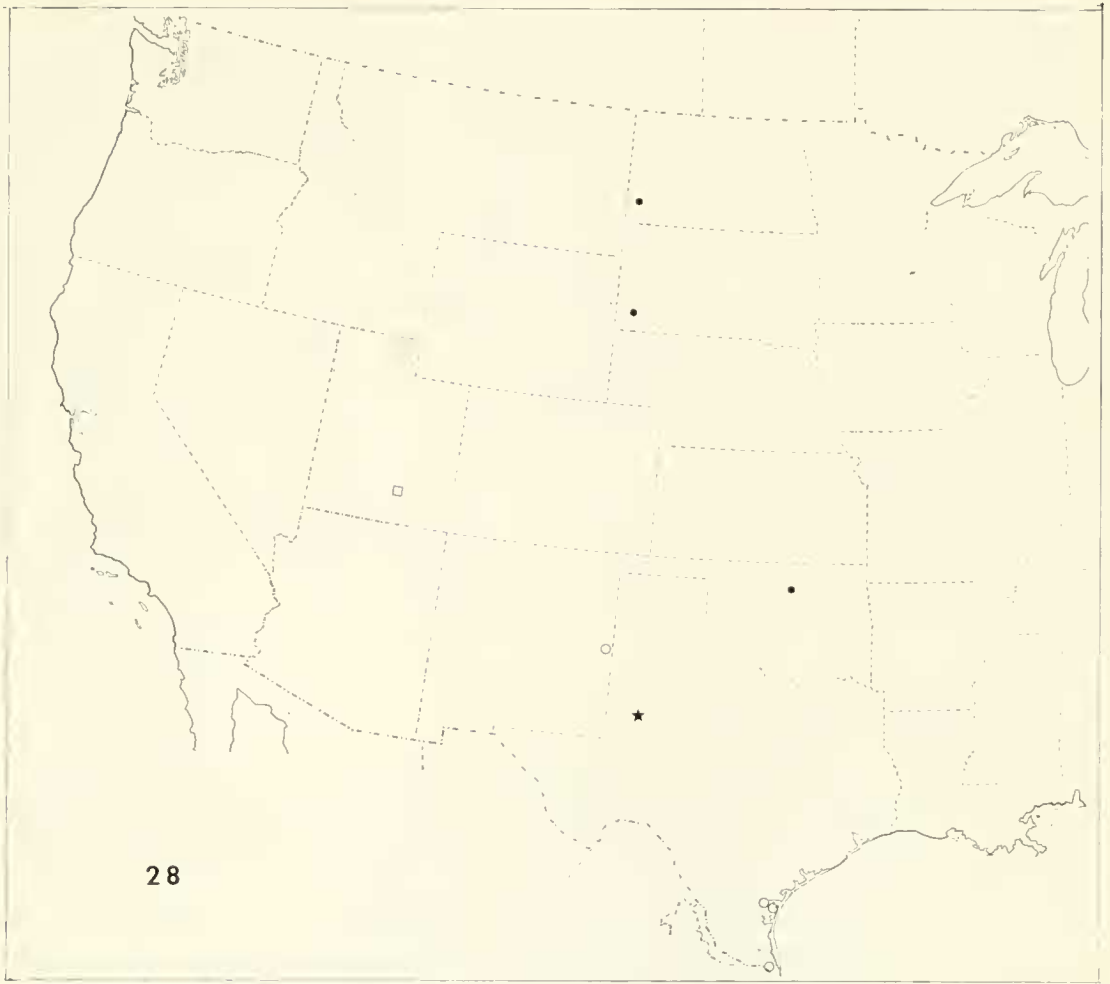


Fig. 28. Distribution of *Aphodius dentiger* (circles), *Aphodius dentigerulus* (dots), *Aphodius formidatus* (star), and *Aphodius henryi* (square).

of rodent, and I suspect that this rodent would be a member of the genus *Neotoma* because *aculeatus* does not possess any of the morphological adaptations that species associated with burrowing rodents usually have.

Specimens examined: Total 11 (fig. 26). NEVADA: Lincoln Co., Oak Springs Summit; Nye Co., Pahrump. UTAH: Millard Co., Delta; Paragonah; Sevier Co., Richfield.

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